

Anatomy and relationships of the papuine land snail *Meliobba shafferyi* Iredale, 1940 (Pulmonata: Stylommatophora: Camaenidae)

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Abstract

Meliobba Iredale, 1940, is a small genus of papuine (arboreal camaenid) snails from Australia and New Guinea, originally diagnosed on shell characters only. The distal reproductive anatomy, head wart, jaw and radula of the type species, *Meliobba shafferyi* Iredale, 1940, are described, providing a wider set of characters on which the generic diagnosis may be based. Anatomical characters of this species are compared with that of *Rhynchotrochus macgillivrayi* (Forbes, 1852) and similarities between the reproductive tracts of the two taxa indicate that they may be closely related. The head wart, which is present in many camaenid genera, is identified as a useful character for determining phylogenetic relationships. It is suggested that the papuine snails may not form a monophyletic group but may represent multiple convergences of shell shape and ecology.

Key words: Camaenidae, *Meliobba*, anatomy

Introduction

Papuines are medium to large arboreal snails found in the forests of eastern Australia, New Guinea and adjacent islands, west to the Moluccas (Clench & Turner, 1962). They are grouped according to conchological and ecological characteristics (elevated shells, tree-dwelling habit), but no morphological synapomorphies define the papuines as a monophyletic assemblage. Although some work has been done on the taxonomy of papuines (Clench & Turner, 1959, 1960, 1962, 1964, 1966, 1968), little is known of their phylogenetic relationships.

Nine species of papuine snails have been recorded from Australia (Smith, 1992), of which five are known from the tropical north-eastern closed forests. The most recently described is *Meliobba shafferyi*, named by Iredale in 1940 from a single shell collected in the Mossman area of North Queensland (Fig. 1). The shell resembled that of no other species from Australia, but Iredale (1940) recognised *M. shafferyi* as having strong affinities with at least one species from southern New Guinea. Although he maintained *Meliobba* as a monotypic genus, he erected a second genus, *Negotobba* Iredale, 1941, to cover similar shells from New Guinea. *Helix goldiei* Brazier, 1884 from Mt Astrolabe and the Owen Stanley Range, New Guinea, was designated as type species. *Meliobba* and *Negotobba* were diagnosed on shell characters alone (Iredale, 1940, 1941).

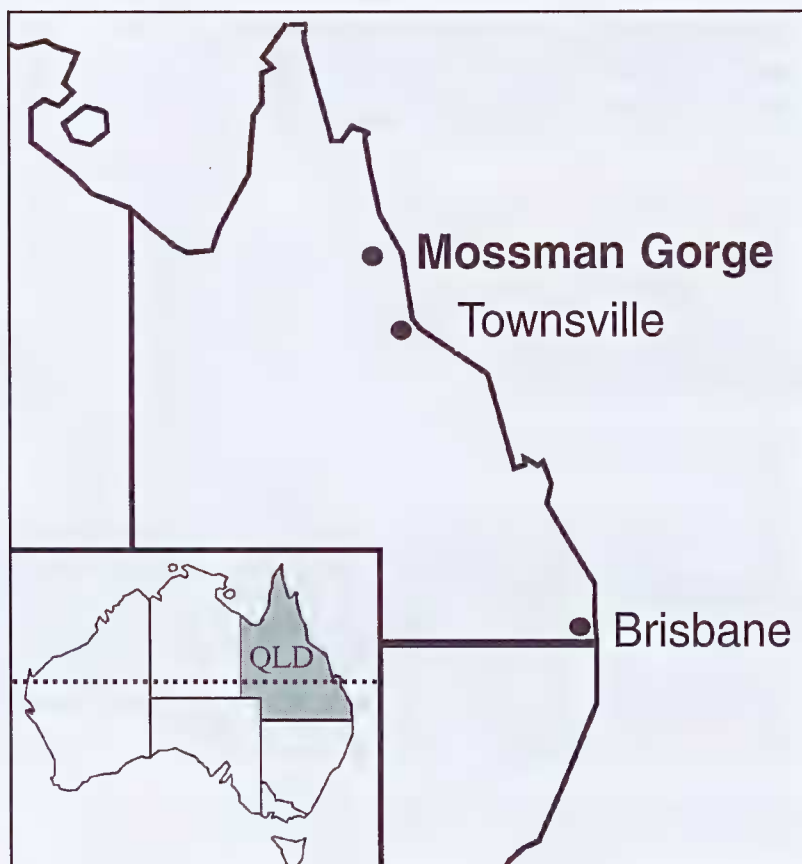


Figure 1. Type locality and known range of *M. shafferyi* (•) at Mossman Gorge, near the township of Mossman.

Clench & Turner (1962) synonymised *Negotobba* with *Meliobba*. They recognised *M. shafferyi* from Australia and five additional species from New Guinea including *goldiei* (Clench & Turner, 1960, 1962). Shells of all six species were described, as was the genital anatomy for those of which they had wet material. However, as anatomical material of neither *shafferyi* nor of *goldiei* was available at that time, Clench & Turner (1962) were unable to describe the type species of either *Meliobba* or *Negotobba* in detail.

The genus *Meliobba* is based on characters of the shell, which may be unreliable. However, character-state convergences in shell shape are so widespread among pulmonates that family- and even genus-level synapomorphies are rare (Goodfriend, 1986; Nordsieck, 1986).

Very few specimens of *Meliobba shafferyi* are held in museums and, until recently, material available for study was restricted to shells only. A single wet specimen, recently deposited in the collection of the Museum of Tropical Queensland, provided an opportunity to describe the anatomy of this species and to examine its relationships within the papuine lineage.

Materials and Methods

A single adult *Meliobba shafferyi* was collected from rainforest at Mossman Gorge, near the township of Mossman, north-eastern Queensland (MTQ MO40193). The specimen was relaxed and killed by freezing (Scott, 1991), fixed in formalin, and stored in 70% ethanol. As this specimen constitutes the only anatomical material currently available, I did not want to damage it unnecessarily. It was impossible to extract the specimen without breaking the shell, so I could not examine the apical reproductive tract, and the specimen was dissected to allow examination of the terminal genitalia only. The terminal genitalia were examined under a dissecting microscope and drawn free-hand (the camera lucida distorts images of large three-dimensional objects, so was not used). The radula was removed and stained with lignin pink for examination under the light microscope, then stored in 70% ethanol with the rest of the specimen. A permanent mount (either slide or SEM stub) was not made for reasons outlined above. The jaw was examined in situ.

Material held in museum collections was also examined to allow comparison of shell and anatomical features. Museum abbreviations are: Australian Museum, Sydney (AM), Museum of Comparative Zoology, Cambridge, Mass. (MCZ), and Museum of Tropical Queensland, Townsville (MTQ).

Material examined

Meliobba shafferyi Iredale, 1940. Holotype, dry, AM C.62205. Queensland, Mossman (= Mossman Gorge).

Meliobba helenae Clench & Turner, 1960. Holotype, dry, AM C.062378. Papua New Guinea, Asai-Simba Divide, Schrader Range, due W of Aiome (5°05'S, 144°50'E). 24 Feb. 1960. Coll: R. Bullmer.

Meliobba mcmichaeli Clench & Turner, 1962. Holotype, dry, AM C.062377. Indonesia, Irian Jaya, Noordweg, Jayapura. 25 Jul. 1959. Coll: R.T. Simon-Thomas.

Meliobba popondetta Clench & Turner, 1962. Holotype, dry, AM C.062376. Papua New Guinea, Mamoo Estate, near Popondetta (8°46'S, 148°19'E). 31 Aug. 1957. Coll: D.F. McMichael.

Rhynchotrochus taylorianus (Adams & Reeve, 1850). 1 live adult, wet, MCZ unreg. Papua New Guinea, Surawaged Mts, Gwengwumgwak nr Wantoat, 3500'. 23 July 1957. Coll. D.F. McMichael.

Rhynchotrochus kubaryi (Möllendorff, 1895). 5 live adults, wet, MCZ unreg. Irian Jaya, New Pionierbivak. Aug. - Oct. 1958. Coll. J.M. Krösschell.

Rhynchotrochus macgillivrayi (Forbes, 1852). 1 live adult, wet, MTQ MO40194. NE Queensland, Etty Bay (17°34'S, 146°05'E). 2 Oct. 1989. Coll: A. Young, P. Meikle.

Results

Meliobba shafferyi Iredale, 1940

Clench & Turner, 1962; Smith, 1992.

Shell

Shell large, lenticular (Fig. 2a), dark horn with lighter sculpture and pale peripheral keel, protoconch dark. Height 27.6 mm, diameter 43.6 mm (measurements include apertural lip). Whorls 5. Spire low, evenly elevated, h/d ratio 0.63. Sutures not impressed. Body whorl keeled. Protoconch sculpture faint, of low radial riblets. Teleoconch sculpture of radial growth lines, overlain by thick plaited wrinkles, which are oblique above the keel and radial below it. Aperture keeled, internal height 15.4 mm, internal width 19.3 mm. Lip glossy white, expanded (max. width 4.4 mm) and reflected, simple except for low tooth on columellar lip. Imperforate.

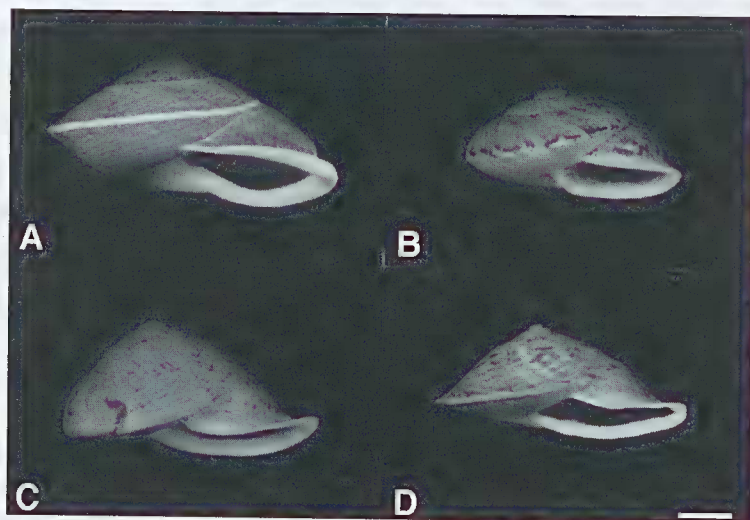


Figure 2. Shells of *Meliobba*. **A.** *M. shafferyi*. **B.** *M. popondetta*. **C.** *M. mcmichaeli*. **D.** *M. helenae*. Scale bar = 10 mm.

External appearance of live animal

Body with orange tubercles on black background. Foot fringe orange. Sole tripartite, with dark grey edges and light grey central portion. Tentacles orange, front of head dark grey. Elongate 'head wart' between upper tentacles (Fig. 3). Mantle collar dark grey to black; mantle over pulmonary cavity unpigmented.

Reproductive tract

Spermoviduct coiling around spermathecal duct. Spermathecal duct massive, attenuated proximally, but otherwise greatly swollen, with thick muscular walls (Fig. 4). Free oviduct approx. 9.5 mm long, 1.8 mm wide, joining vagina at right angle. Vagina approx. 9 mm long, 3.8 mm wide. Interior vaginal walls lined with smooth longitudinal ridges, becoming convoluted at opening of free oviduct, continuing in duct of spermatheca as crenulate ridges. Internal differentiation in sculpture of walls of vagina and spermathecal duct distinct.

Vas deferens 1.2mm wide adjacent to vagina on female side (Fig. 4), 0.6 mm on male side, enters epiphallus close to small (1.5 mm) recurved flagellum (Fig. 5). Epiphallus tubular, longer than penis (epiphallus = 44 mm). Penis sheath absent, but vas deferens, epiphallus and penis bound together by thick mesenteries. Penis papilla large (9 mm long), occupying almost whole of penis lumen. Papilla broad, flattened, coiled into conical shape (Fig. 6). Papilla heavily sculptured. Sperm channel from opening of epiphallus into penis to proximal papilla. Sculpture of penis lining (external wall when everted) similar to that of penis papilla but less pronounced. Penis wall thin proximally (around penis papilla), much thicker distally.

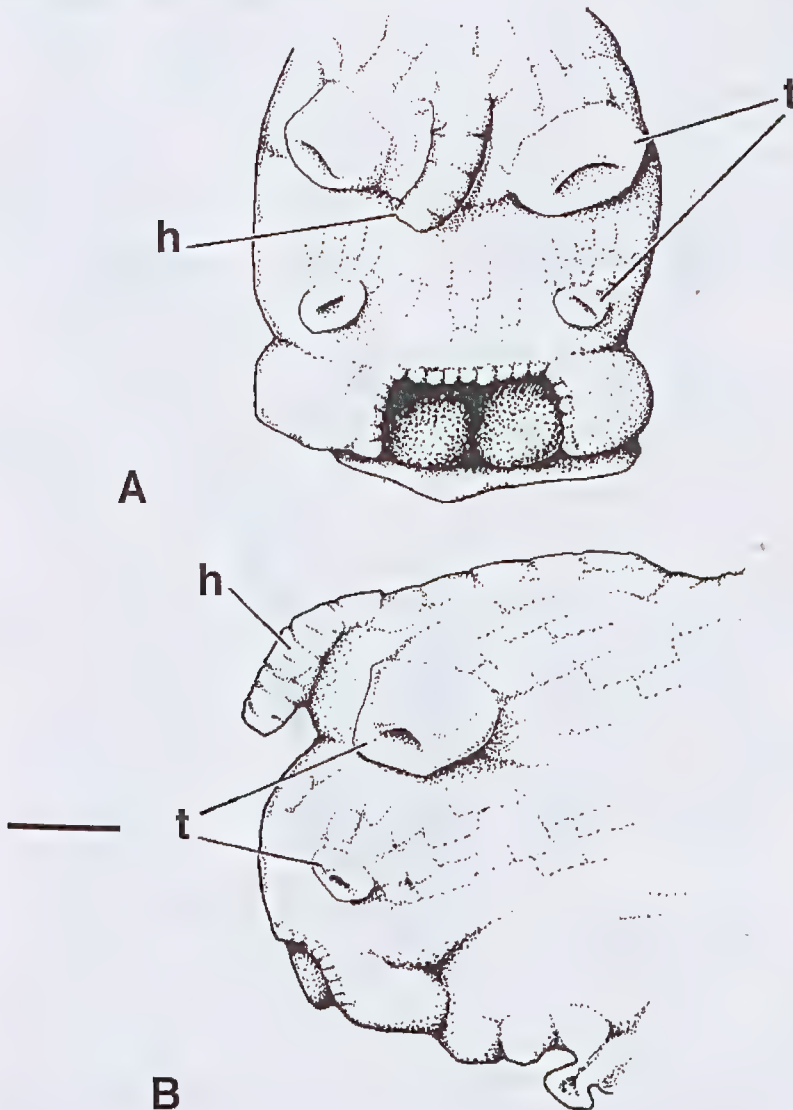


Figure 3. Head wart of *M. shafferyi*. A. Anterior view. B. Lateral view. Scale bar = 2 mm. Abbreviations: hw, head wart; t, tentacles.

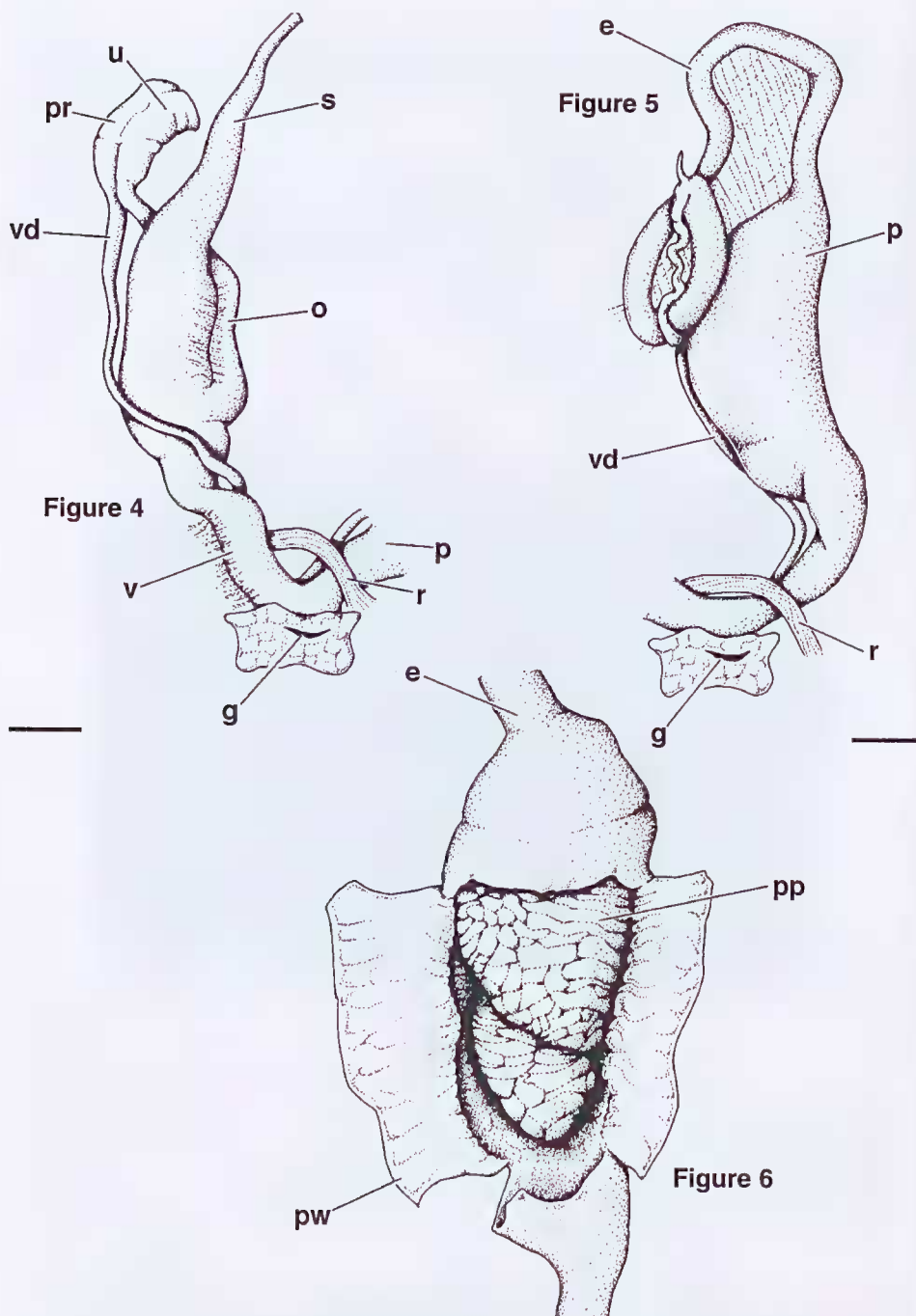


Figure 4. Female genitalia of *M. shafferyi*. Scale bar = 2 mm. Abbreviations: g, genital opening; m, tentacular retractor muscle; o, free oviduct; p, penis; pr, prostate; s, spermathecal duct; u, uterus; v, vagina; vd, vas deferens. **Figure 5.** Male genitalia of *M. shafferyi*. Scale bar = 2 mm. Abbreviations: e, epiphallus; g, genital opening; m, tentacular retractor muscle; p, penis; vd, vas deferens. **Figure 6.** Penis interior of *M. shafferyi*. Scale bar = 2 mm. Abbreviations: e, epiphallus; pp, penis papilla; pw, wall of penis.

Jaw and radula

Jaw 1.1 mm deep, 3mm wide, strongly curved, with 12 low narrow ribs. Central tooth of radula with spatulate cusp, laterals similar with minor asymmetry, marginals not observed but cusps of transitional teeth demonstrate asymmetry with small endocone and distinct ectocone.

Discussion

Shell shape in *Meliobba shafferyi* generally resembles that of other species assigned to *Meliobba* with minor differences in the width of the lip, shape of the aperture, and the degree of umbilical closure. In none of the three species examined is the lip as wide as that of *M. shafferyi*, nor is the umbilicus wholly occluded, although that of *M. helenae* is almost closed (Clench & Turner, 1960, pl. 3, 1962, pl. 2-3). There is also some difference between species in the curve of the dorsal body whorl immediately behind the lip. In *M. shafferyi* and *M. popondetta*, the external shell wall is convex like the preceding portion of the body whorl, as is the palatal lip (Fig. 2a,b); in *M. mcmichaeli* and *M. helenae* the wall is concave, with a corresponding curve in the lip and constriction in the aperture (Fig. 2c, d). This can also be seen in illustrations of *M. goldiei* and *M. lintschuana* (Clench & Turner, 1962: pl. 2-3). However, it should be remembered that the sample sizes are very small (in most cases, holotype only), so the variation within species can not be determined.

Despite marked similarities in shell shape, differences between the reproductive tract of the type species and of those illustrated for congeneric species (Clench & Turner, 1962, figs. 7-9; 1966, figs. 1-6) suggest that *Meliobba* sensu Clench & Turner is a complicated genus and may not be a monophyletic group. The base of the spermathecal duct of *M. shafferyi* is grossly swollen and the duct is proportionately longer than that recorded from other species of *Meliobba* except for *M. helenae* (Clench & Turner, 1962, figs. 7-9). The epiphallus is slender (readily distinguishing it from the penis) and the penis papilla is large, unlike that of the other congeneric species for which anatomical data are available (Fig. 6; Clench & Turner, 1962, figs. 7-9). The epiphallic flagellum is short and recurved, a condition also found in *M. mcmichaeli* and *M. popondetta* but not in *M. helenae* (Clench & Turner, 1962). Character states display a 'mosaic' distribution with the result that it is difficult to diagnose the genus satisfactorily on reproductive characters. There appears to be no well-defined anatomical synapomorphy uniting the group, a situation which reflects the taxonomic problems associated with Camaenidae as a whole (Scott, 1996).

The terminal male and female genitalia of *Meliobba shafferyi* show many similarities to those structures considered diagnostic of *Rhynchotrochus* (Clench & Turner, 1966). In both taxa the spermathecal duct is long and attenuated, the free oviduct is swollen at the base, a short, recurved epiphallic flagellum is present at the junction of epiphallus and vas deferens, the penis wall (penis sheath of Clench & Turner, 1966) is thin proximally and much thicker distally, and the penis papilla is large with a marked sperm gutter along one side (Clench & Turner, 1966).

Radular teeth are comparable to those of other species of *Meliobba* and also of *Rhynchotrochus* (Clench & Turner, 1962, fig. 3, 1966, figs. 1, 4-6), with a spatulate central tooth and broad mesocone on the lateral teeth.

	<i>M. shafferyi</i>	<i>M. helenae</i>
body	orange on black	dark brown
tentacles	orange	nearly black
upper surface of foot	orange	yellow
sole	light grey	deep ivory
edge of sole	dark grey	yellow

TABLE 1. Colour patterns in living *M. shafferyi* and *M. helenae* (data from Clench & Turner, 1960)

External features of *M. shafferyi* may provide the most important clues to its evolutionary relationships, but so little information on New Guinea and Australian papuinines is currently available that no conclusions can be drawn, only comparisons made. The striking colour pattern on the living animal (orange on black) differs strongly from that reported for *M. helenae*, the only other *Meliobba* observed alive (Clench & Turner, 1960) (Table 1). Bright and contrasting colours are rare among snails, so this unusual pattern may be significant phylogenetically.

The 'head wart' of *M. shafferyi* is also distinct. It is elongate and tubular, resembling neither the head wart structure of other Australasian camaenids and Asian Bradybaenidae (Taki, 1935; Solem, 1992; Scott, unpubl. data) or the cephalic (frontal) organ of the African Urocyclidae (Binder, 1969). It is such a large and obvious structure that if it were present in *M. helenae* it would certainly have been recorded by Clench & Turner (1960) when they examined their living specimen. The tropical Australian species *Rhynchotrochus macgillivrayi* also appears to possess a head wart, but this is a low circular self-coloured structure similar to that of other Australasian camaenids, such as *Rhagada* of northern Western Australia (Solem, 1985) and the hadroid camaenids of eastern Queensland (Solem, 1992; Scott, unpubl. data). It does not resemble that of *M. shafferyi* in any way except position. Evidence from reproductive tract characters suggests that *Meliobba* and *Rhynchotrochus* are closely related, the structure of the head wart suggests that they are not, and conchological evidence is equivocal.

Elaborate structures, such as the head wart, are useful in phylogenetic reconstructions, whereas characters of the shell are more likely to exhibit convergence and confuse analyses (Cain, 1982). The head wart is present in many Australian camaenids including *Hadra* and its allies (Solem, 1992; Scott, unpubl. data), *Rhagada* (Solem, 1985), the eastern Asian *Camaena* and some central Australian genera (Solem, 1993). It is also found in the Asian Bradybaenidae, the family from which it was first described (Taki, 1935; Takeda, 1982). In Australian camaenids the organ varies from a patch of specialised tubercles to a fully-eversible wart which can be retracted into a transverse slit when not in use (Solem, 1992; Scott, unpubl. data). States appear to be discrete, so each state may be regarded as a synapomorphy uniting taxa in distinct lineages. The head wart of *Meliobba shafferyi* is more strongly developed than that of other Australasian camaenids and so may be used to define another lineage within the group. Whether this structure occurs in *Papuina sensu stricto*

is not known, but its study, together with that of characters of the genitalia, pallial complex and nervous system, may determine whether or not the papuinines represent a true clade.

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References

- Binder, E. (1969). Cephalic accessory sexual organ of *Gymnarrion*: speciation and phylogeny (Pulmonata, Helicarionidae). *Malacologia* 9: 59-64.
- Cain, A.J. 1982. On homology and convergence, in 'Problems of phylogenetic reconstruction.' Joysey, K.A. and Friday, A.E. (eds.), Systematics Association, London.
- Clench, W.J. & Turner, R.D. 1959. Two new genera of land molluscs (Papuinae) from the Central Highlands of New Guinea. *Journal of the Malacological Society of Australia* 1(3): 4-9.
- Clench, W.J. & Turner, R.D. 1960. A new *Meliobba* from the Schrader Range, New Guinea. *Journal of the Malacological Society of Australia* 1(4): 30-31.
- Clench, W.J. & Turner, R.D. 1962. Monographs of the genera *Papustyla*, *Forcatia* and *Meliobba* (Papuinae: Camaenidae). *Journal of the Malacological Society of Australia* 1(6): 3-33.
- Clench, W.J. & Turner, R.D. 1964. Monographs of the genera *Megalacron* and *Rhytidoconcha* (Papuinae: Camaenidae). *Journal of the Malacological Society of Australia* 1(8): 36-70.
- Clench, W.J. & Turner, R.D. 1966. Monograph of the genus *Rhynchotrochus* (Papuinae: Camaenidae). *Journal of the Malacological Society of Australia* 1(9): 59-95.
- Clench, W.J. & Turner, R.D. 1968. Monograph of the genus *Letitia* (Papuinae: Camaenidae). *Journal of the Malacological Society of Australia* 1(11): 32-49.
- Goodfriend, G.A. 1986. Variation in land-snail shell form and size and its causes: a review. *Systematic Zoology* 35: 204-223.
- Iredale, T. 1938. Basic list of the land Mollusca of Australia - part III. *Australian Zoologist* 9: 83-124.
- Iredale, T. 1940. A New Guinea land shell in Queensland. *Australian Naturalist* 10: 239-240.
- Iredale, T. 1941. A basic list of the land Mollusca of Papua. *Australian Zoologist* 10: 51-94.
- McMichael, D.F. 1958. A new tree-snail from North Queensland. *Journal of the Malacological Society of Australia* 1(2): 41-43.
- Nordsieck, H. 1986. The system of the Stylommatophora (Gastropoda), with special regard to the systematic position of the Clausiliidae. II. The importance of the shell and distribution. *Archiv für Molluskenkunde* 117: 93-116.
- Scott, B.J. 1991. Freezing technique for relaxing and killing terrestrial snails. *Australian Shell News* 77: 2.
- Scott, B. 1996. Phylogenetic relationships of the Camaenidae (Gastropoda: Pulmonata: Stylommatophora). *Journal of Molluscan Studies* 62: 65-73.
- Smith, B.J. 1992. Non-marine Mollusca, in *Zoological Catalogue of Australia*, 8. Houston, W.W.K. (ed.). Australian Government Publishing Service, Canberra.

- Solem, A. 1985. Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). V. Remaining Kimberley taxa and addenda to the Kimberley. *Records of the Western Australian Museum, Supplement* 20: 707-981
- Solem, A. 1992. Camaenid land snails from southern and eastern South Australia, excluding Kangaroo Island. *Records of the South Australian Museum, Monograph series* 2: 1-325
- Solem, A. 1993. Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae) VI. Taxa from the Red Centre. *Records of the Western Australian Museum, Supplement* 43: 983-1459.
- Takeda, N. 1982. Notes on the fine structure of the head-wart in some terrestrial snails. *Veliger* 24: 328-330.
- Taki, I. 1935. Notes on a warty growth on the head of some land snails. *Journal of Science of the Hiroshima University, Series B, Division 1* 3: 159-183.